

A description of the larva and discussion of radiation in the phytotelm breeding damselfly genus *Papuagrion* in New Guinea (Odonata: Zygoptera: Coenagrionidae)

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The larva of *Papuagrion* is described and illustrated for the first time based on two specimens collected near Goroka, Papua New Guinea. The larvae were identified by matching the mitochondrial marker COI with that of an adult specimen collected at the same locality. The larvae were found in the leaf axils of *Pandanus* trees which agrees with earlier observations that adults are often encountered away from water, in the vicinity of *Pandanus*. Larvae collected from water pooled in the leaf bracts of several *Pandanus* trees in the Muller Range (PNG) are also thought to belong to the genus *Papuagrion*. Based on these records and further observations it is considered likely that all species of *Papuagrion* live in phytotelmata and that most or even all are found in *Pandanus* trees. *Papuagrion* is derived from a Papuan radiation of the genus *Teinobasis*, members of which inhabit standing or slow-flowing and often muddy waters, where the larvae probably develop, suggesting that the colonisation of phytotelmata offered by *Pandanus* trees has led to the radiation of *Papuagrion*, possibly because of the discrete and scattered nature of suitable habitats. The larvae show little difference morphologically from the few known *Teinobasis* larvae. The colonisation of phytotelmata as a larval habitat sometimes followed by an extensive radiation seems to have occurred independently several times within Coenagrionidae.

Keywords: Odonata; Zygoptera; Coenagrionidae; larval description; phytotelmata; New Guinea

Introduction

The genus *Papuagrion* currently includes 26 described species which are restricted to New Guinea and the islands of Biak-Supiori and Japan. They are found from sea-level to almost 3000 m. The genus belongs to the so called ridge-faced Coenagrionidae, a large, probably monophyletic subdivision of the Coenagrionidae characterised by having a sharply angulated frons and lacking paired postocular spots (Dijkstra, Kalkman, Dow, Stokvis, & van Tol, 2013). It is closely related to the large genus *Teinobasis* that occurs from Peninsular Malaysia to northern Australia and the Solomon Islands. *Papuagrion* is differentiated from *Teinobasis* by the presence of an inferior tooth on the tarsal claw and by R4 arising before the subnodus instead of at or a little distal from the subnodus (Michalksi & Oppel, 2007). These characters are occasionally unreliable but in practice members of the genus are easy to recognise as they have a characteristic dusky coloration and are much larger and sturdier in build than most species of *Teinobasis*.

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In his description of *P. pandanicolum* Lieftinck (1949) states that the “larva of this, and probably several other species of *Papuagrion*, lives in the water which collects between the bases of the leaves of *Pandanus*. Dr. Toxopeus, whilst collecting at Moss Forest Camp, found one young and one matured larva of *pandanicolum*, the last mentioned one having been taken in the act of emerging” (see Toxopeus, 1939 for details of this observation). He furthermore states that the specimen will be described in a paper discussing the origin of the “pandanicolous habits”. However this paper was never published and the remark on the habitat of *Papuagrion* was overlooked by workers interested in Odonata breeding in phytotelmata (e.g. Corbet, 1983; Kitching, 2000). Information on the habitat of *Papuagrion* published since has been scarce and of rather general nature indicating that they are found in or near forest. The first to publish more detailed habitat information was Oppel (2005) who provided information for three species:

- *Papuagrion* sp. nov. A: “A copulating pair was found next to a sunny clearing in the forest, perching on vegetation 2 m above the ground. There were no water sources nearby, but several *Pandanus* sp. trees, which might serve as larval habitat for that species.” (Oppel, 2005).
- *Papuagrion* sp. D: “... a female of this species was found near *Pandanus* sp. trees. A male of this species was caught along a medium sized creek, but this might have been foraging habitat, which might explain the scarcity of encounters. The same (?) species was also found in Herowana, either along ditches or near shady puddles in the forest.” (Oppel, 2005).
- *Papuagrion occipitale*: “At CMBRS, a species that resembled *P. occipitale* was fairly common, but usually only found on warm and sunny days when individuals were basking in sunny spots in the forest. Some of these areas were next to small creeks, but most individuals were found far away from water, and there is a possibility that this species, too, is affiliated with *Pandanus* sp. trees. In Herowana only one individual was found next to a creek.” (Oppel, 2005).

The species mentioned as *Papuagrion* sp. nov. was later described by Michalski and Oppel (2007) as *P. carcharodon* with the comment “The male of the new species was taken on a forest track in a sunny clearing surrounded by *Pandanus* trees, and with no water in the immediate area.” Another reference to the habitat of *Papuagrion* is given by Kalkman (2008) who states that, for *P. prothoracale*, *P. occipitale* and a third unidentified species at Borne (Central Mountain Range, Indonesia), nearly all specimens were caught at a stand of large *Pandanus* trees where they remained in the canopy and did not seem to be associated with the muddy brook running below it. A similar observation was made for *P. occipitale*, *P. prothoracale* and an undescribed *Papuagrion* species (here referred to as *Papuagrion* sp. A) on the island of Japan where nearly all specimens were also found at stands of *Pandanus* while a fourth species, *P. magnanimum*, was encountered near a brook, although not clearly associated with it (pers. obs. V.J. Kalkman). Three new species recently described from the Hindenberg Wall at 1770–1820m asl were all observed away from water, near forest in which *Pandanus* trees were plentiful (Orr & Richards, 2016).

Methods

Site and collection of material

On 19 September 2009 Piotr Naskrecki cut down a *Pandanus* tree during the Muller Range Expedition at Camp Apalu Reke, PNG (see Kalkman, Theischinger, & Richards, 2011 for locality details) in order to inspect the canopy for the presence of katydids. In the leaf axils three larva of Zygoptera were found which were shown to the first author. In the following days several other *Pandanus* trees were sampled. A large *Pandanus* standing in the open and a small *Pandanus* at



Figure 1. Small *Pandanus* tree at Muller Range (PNG). The leaf axils of which contained larvae of *Papuagrion*. Photograph VJK.

the forest edge did not contain any larvae. Larvae were found in a small *Pandanus* (Figure 1) and a tall *Pandanus* (Figure 2) standing within the forest. The sampling is rather destructive as it is necessary to cut down the tree and remove all leaves using a machete to properly inspect the leaf axils (Figure 3).

All larvae were found near the base of the leaves where the leaves are pale green to yellow and all were found on relatively clean leaves (e.g. not holding detritus or small fallen leaves). The larvae were found to be well able to walk on the leaves and might have spent only part of their time in the water (Figure 4). Despite intensive searching no adults of this species were found. Two weeks later on 29 September 2009 a small *Pandanus* tree near Goroka, Eastern Highland Province, PNG, was cut down and the leaf axils were checked, resulting in the discovery of two larvae (Figure 5). In the vicinity an adult male *Papuagrion marijanmatoki* Orr & Richards, 2016 was collected. DNA samples were taken from the male and the two larvae resulting in the positive identification of the larva as *P. marijanmatoki*.

Molecular analyses

The relationship of *Papuagrion* with other genera of the ridge-faced Coenagrionidae is shown in Figure 6. This figure is an adaptation of figure 2 presented in Dijkstra et al. (2013). The two larvae from Goroka showed a 99.7% match with the adult of *Papuagrion marijanmatoki* collected at



Figure 2. Large *Pandanus* tree at Muller Range (PNG). The leaf axils of which contained larvae of *Papuagrion*. Photograph VJK.



Figure 3. The sturdiness of the leaves and the large spines on the leaf edges mean that the only way to properly inspect the leaf axils is to cut down the tree and remove all leaves using a machete. Photograph VJK



Figure 4. The larvae of *Papuagrion* were found able to walk out of water. Photograph S.J. Richards.



Figure 5. Small *Pandanus* tree at Goroka (PNG). The leaf axils of which contained larvae of *Papuagrion*. Photograph VJK.

Goroka. Figure 6 shows that these larvae are more closely related to *P. marijanmatoki* than to any other of the included species of *Papuagrion*. This tree is based on a simple neighbour-joining analyses and should not be regarded as b22a phylogeny of the group. A description of the extraction of DNA, the editing of sequences and primer combinations used is given in Orr and Dow (2015a, 2015b). GenBank accession numbers for sequences not previously published are provided in Table 1; others can be found in Dijkstra et al. (2013).

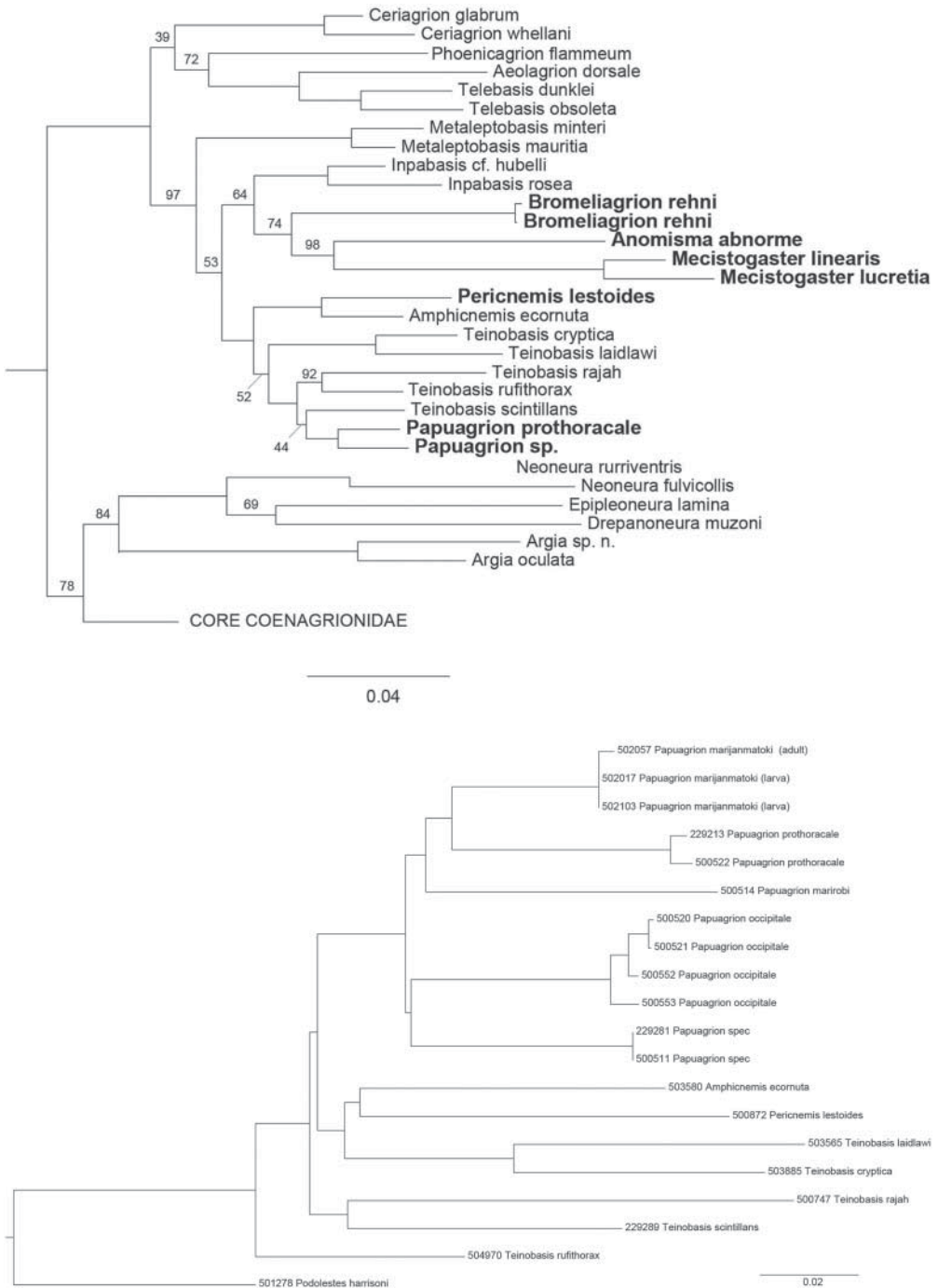


Figure 6. (a) Phylogenetic reconstruction from the combined Bayesian analysis of 28S, 16S and COI. Posterior probabilities are shown (as percentages) only if below 100%. Genera which are known to breed in phytotelmata are shown in bold. Adaptation of Dijkstra et al. (2013, figure 2e); see there for details on methods. (b) Neighbour-joining COI gene tree using uncorrected p-distance for a selection of genera belonging to the ridge-faced Coenagrionidae (*Amphicnemis*, *Teinobasis* and *Pericnemis*) with *Podolestes harrisoni* used as outgroup. All voucher specimens have a six-digit collection number with an RMNH.INS. prefix; this prefix is omitted in the figure for clarity.

Table 1. GenBank accession numbers for previously unpublished COI sequences used in the analysis.

Species	RMNH.INS	Country	Location	GenBank accession number
<i>Papuagrion marijanmatoki</i>	RMNH.INS.502017	Papua New Guinea	“Eastern Highlands, Goroka”	KX233621
<i>Papuagrion marijanmatoki</i>	RMNH.INS.502103	Papua New Guinea	“Eastern Highlands, Goroka”	KX233622
<i>Papuagrion marijanmatoki</i>	RMNH.INS.502057	Papua New Guinea	“Eastern Highlands, Goroka”	KX233623
<i>Papuagrion occipitale</i>	RMNH.INS.500521	Indonesia	“Papua, Star Mountains”	KX233624
<i>Papuagrion occipitale</i>	RMNH.INS.500553	Indonesia	“Papua, Yapen”	KX233625
<i>Papuagrion occipitale</i>	RMNH.INS.500520	Indonesia	“Papua, Star Mountains”	KX233626
<i>Papuagrion occipitale</i>	RMNH.INS.500552	“Indonesia, Abepura”	Papua	KX233627
<i>Papuagrion prothoracale</i>	RMNH.INS.500522	Indonesia	“Papua, Star Mountains”	KX233628
<i>Papuagrion</i> sp.	RMNH.INS.500514	Indonesia	“Papua, Yapen”	KX233629
<i>Papuagrion</i> sp.	RMNH.INS.500511	Indonesia	“Papua, Supiori”	KX233630
<i>Papuagrion</i> sp.	RMNH.INS.229281	Indonesia	“Papua, Biak”	KX233631

Description of larvae

Papuagrion marijanmatoki Orr & Richards, 2016

Figures 7, 8a–i

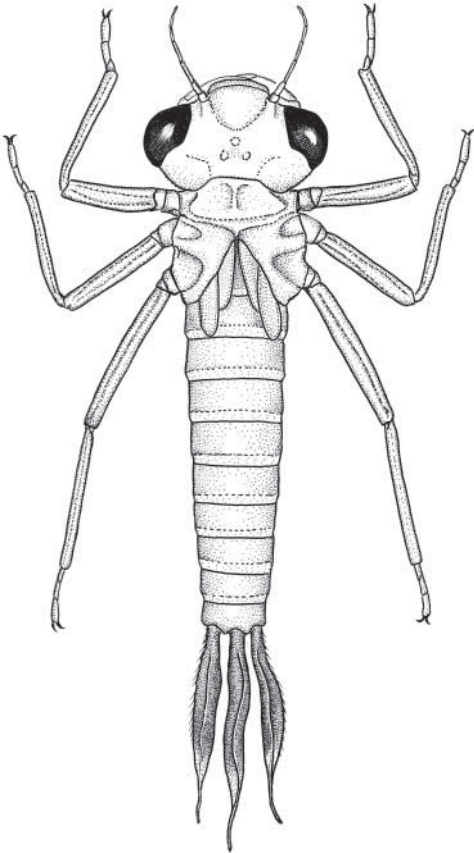


Figure 7. *Papuagrion marijanmatoki*, ?F-2 larva, ♀, habitus.

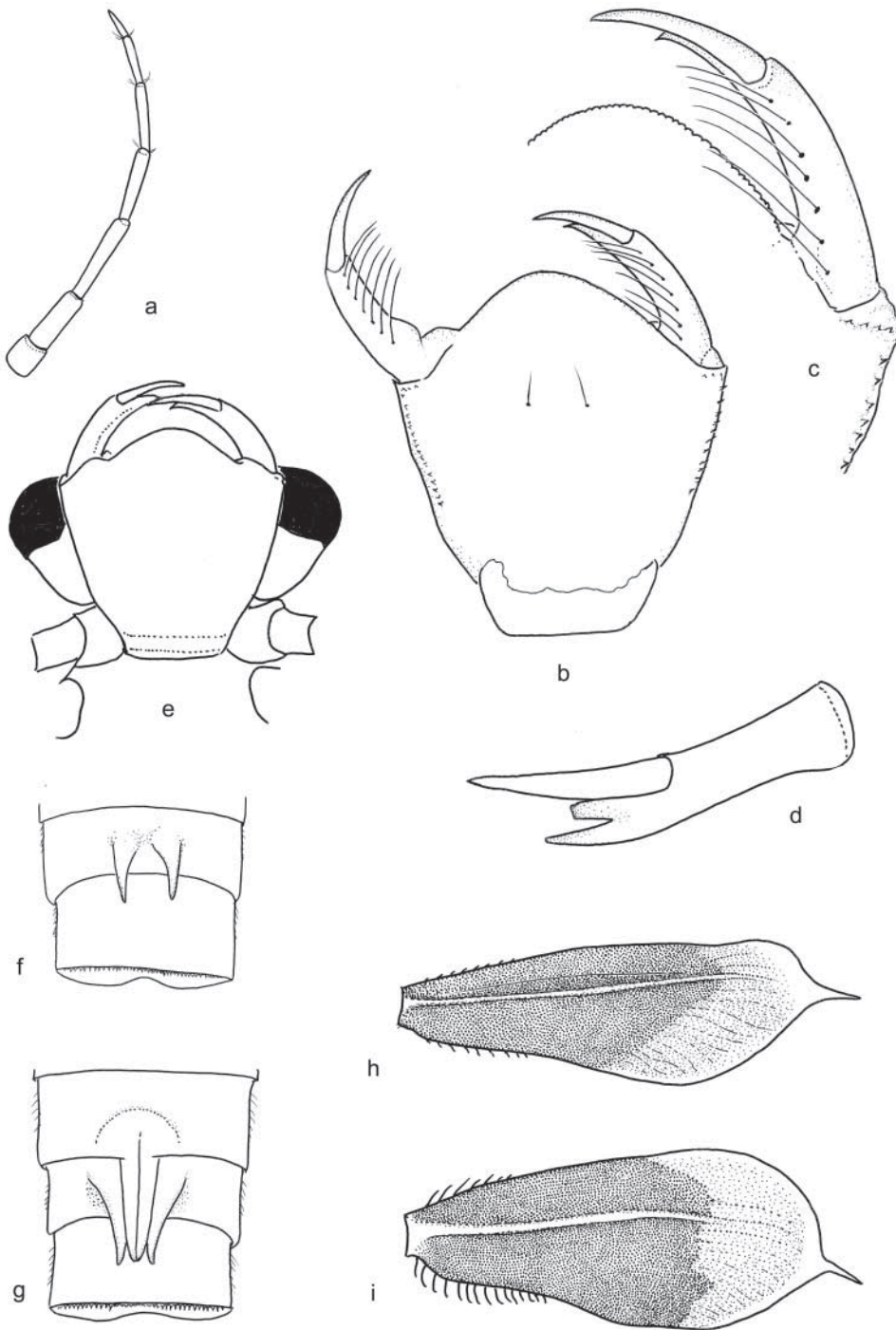


Figure 8. *Papuagrion marijanmatoki*, ?F-2 larva: (a) detail antenna; (b) mask in dorsal view; (c) detail anterior margin of prementum and right labial palp; (d) lateral outer detail of labial palp; (e) ventral view of head, mask and prothorax; (f) ventral view S9-S10 showing ♂ gonapophyses; (g) ventral view S8-S10 showing ♀ gonapophyses; (h) ♀ larva median caudal lamella in lateral view; (i) ♀ larva left caudal lamella in lateral view.

Material

One ♂ F-2(?) larva, one ♀ F-2(?) larva, both Papua New Guinea, Goroka — 06.0205°, 145.4097°, 19 September 2009 from water collected in leaf axils of *Pandanus*, leg V. J. Kalkman.

Description

In general appearance a small, rather short-legged zygopteran of medium build and typical coenagrionoid appearance. Postocular lobes of head well developed and rounded. Caudal lamellae foliate, somewhat broadened. Coloration overall neutral brown without distinct markings. Body surface relatively smooth bearing only sparse, very fine setae. General appearance (Figure 7) rather squat, probably as a result of immaturity.

Head in dorsal view (Figure 7) broad and robust, roughly squashed pentagon in outline, postocular lobes very well developed, rounded, bearing short heavy setae posterolaterally, projecting posteriorly so that the outline of head is deeply excavated posteriorly; labium and palps easily visible projecting beyond labrum and laterally; antennae (Figure 7a) 7-segmented, S1–7 length ratios: 1, 1.6, 2.9, 2.5, 1.6, 1.5, 1.3. Compound eyes moderately large. Mandibles not evident in dorsal view, being concealed by labrum and antennal bases. Mandibles seen in ventral view rather squat with well-developed long teeth on each incisor lobe; right mandible with five distinct separate long incisor teeth but molar field smooth; left mandible with three distinct separate long incisor teeth, two vestigial and one small prominent tooth in molar field. Prementum (Figure 8b) short and broad, somewhat tapered toward base, bearing single pair of long, strong setae seated post-medially; anterior margin (ligula) strongly produced to form a smooth rounded arch, its margin bearing fine crenulations; median cleft absent; lateral margins of prementum bearing short thick-based spines in distal three-fifths, several such spines also present submarginally around base of palps; labial palp (Figure 7c, d) rather short, terminating an elongated pair of ventral processes, the lower one acute, the upper narrowly securiform and considerably shorter, the two lobes separated by a deep incision (Figure 8d). Palp bearing seven long, strong, inwardly directed setae and a rather short stout movable hook, seated well back from its apex. Articulation of mask reaching hind margin of procoxae when retracted (Figure 7e). Legs moderately short; femora stout and somewhat angular, without obvious banding or spines; tibiae thin with only very fine sparse setae. Wing pads (in these immature specimens) just reaching hind-margin of S2. Abdomen unmarked, smooth, gradually tapered posteriorly. Cerci very small, not visible in dorsal view. Male gonapophyses long, overlapping basal quarter of S10 (Figure 7f). Female gonapophyses broad, reaching to middle of S10 (Figure 7g). Inner and outer gonapophyses subequal in length. Caudal lamellae (Figure 8 h, i) clearly dorsolaterally flattened, foliate and moderately broad, especially the median lamella (Figure 2 h); all well tracheated, darkened for basal two thirds with short terminal filament; median lamella about two-fifths length of abdomen.

Measurements (mm)

Total length (without caudal lamellae) 9.4–9.8; maximum width of head 2.91–2.95; hind femur 2.4–2.5; right lamella 3.2; median lamella 3.35.

Remarks

Because both specimens are immature, the habitus is somewhat squat in appearance. Slight allometric differences might also occur in relative length of legs, gonapophyses and caudal appendages when compared with an F-0 larva. However in all significant diagnostic features we

consider these specimens characterise the genus well. These features differ only in minor ways from those described for *Teinobasis* cf. *nigrolutea*. The latter was described with some expressed doubt by Lieftinck (1962) as *T. ariel* but Paulson and Buden (2003) suggest that the specimen described is in fact *T. nigrolutea*, for which reason we refer to it as *T. cf. nigrolutea*. The shape of the head is almost identical; the prementum is of a very similar shape with the exception that the anterior margin is produced further and more rounded; the distal armature on the labial palp is more strongly developed and the palp bears seven rather than four long setae; the caudal lamellae are very similar in overall outline but that of *P. marijanmatoki* bears short terminal filaments. Lieftinck (1962) does not comment on the colour of the caudal lamellae but his drawing suggests they are less pigmented than in *P. marijanmatoki*.

Discussion

The previously published information on the habitat of *Papuagrion* is entirely consistent with the discovery of larvae of *P. marijanmatoki* in the leaf axils of *Pandanus* trees. For four other species (*carcharodon*, *occipitale*, *prothoracale*, *Papuagrion* sp. A) authors noted that they have been observed sitting on or in close proximity to *Pandanus* trees (Kalkman, 2008; Michalski & Oppel, 2007; Oppel, 2005; Orr & Kalkman, forthcoming). For other described species no clear habitat information has been given in the literature but in some cases it is noted that they were observed away from water. Additionally, *Papuagrion* has never been documented in the literature or otherwise to exhibit territorial, mating or oviposition behaviour at normal aquatic habitats such as streams or ponds (pers. obs. Dan Bartha, Vincent Kalkman, John Michalski, Stephen Richards). Based on this it seems likely that all species of *Papuagrion* breed in phytotelmata and are largely confined to *Pandanus* trees.

Papuagrion is most closely related to the large and possibly polyphyletic genus *Teinobasis*. The larva of only three of the 75 known species of *Teinobasis* have been described, all three from Pohnpei, Micronesia: *T. ariel* and *T. fortis* by Paulson and Buden (2003) and *T. cf. nigrolutea* by Lieftinck (1962). The latter was originally described as *T. ariel* but its identity is questioned by Paulson and Buden (2003). The description of this larva stated the larva was found “in *Freycinetia*” (family Pandanaceae) and the occurrence of damselfly larva in phytotelmata on Pohnpei is further evidenced by a remark by Gressitt (1954) that “damselfly naiads” were found in “the accumulated water in the axils of *Pandanus* and *Freycinetia* leaves”. This led Lieftinck (1962) to suggest that “it is not unlikely that the entire group [*Teinobasis*] in Ponape is specialised to arboreal habits”, an idea however which proved to be incorrect as the larvae of the other two species whose larva are described were found in normal aquatic habitats (Paulson & Buden, 2003). The known habits of adults from other species of *Teinobasis* from Malaysia, Indonesia and Papua New Guinea suggest that all other species are found at normal aquatic habitats, although admittedly no data on larva are available (pers. Obs. Rory Dow, Vincent Kalkman, Albert Orr, Stephen Richards). The larval structure of the three species of *Teinobasis* whose larva are known does not differ substantially from the *Papuagrion* larva described here except in having fewer palpal setae. Indeed, Paulson and Buden (2003) identify significant variation in the shape of the mask and head in the three *Teinobasis* species known; *Teinobasis fortis* in particular stands out in this regard, having a very robust head and mask; it also has acuminate caudal lamellae, as in *Papuagrion marijanmatoki*, but unlike in *P. marijanmatoki* they are very narrow (Paulson & Buden, 2003). As a rule, phytotelm-dwelling Zygoptera tend to exhibit stalked, broad leaf-like caudal lamellae coloured black or purple, short legs, large size and numerous setae on the labial palp (Ramirez, 1997). This latter character is present in the larvae of *Papuagrion* even though the specimens are immature, and presumably relates to an overall larger size achieved by the

F-0 larvae relative to non-phytotelm-breeding *Teinobasis*. Also it seems likely that the caudal lamellae are more strongly pigmented in *Papuagrion*. Moreover as Ramirez (1997) noted, not all phytotelm-breeding species conform to the standard pattern, especially in the shape of the gills which, while always expanded, are often not strongly so, especially among species breeding in bromeliads (see e.g. *Bromeliagrion rehni*, Torreias Neiss, Hamada, Ferriera-Kepler, & Lencioni, 2008). One possible reason for this may be the physical properties of different types of phytotelmata. Orr (1997) demonstrated that the oxygen levels in buttress pans at the levels inhabited by *Pericnemis dowi* (identified as *P. triangularis*), which does have greatly expanded, heavily pigmented gills (Orr 1994), was about 0.2 ppm with a thin layer of 1–1.5 ppm at the surface. It is possible that water collected in the leaf axils of *Pandanus*, and also in bromeliads, supports higher oxygen levels partly because the architecture of the plant exposes a greater surface area of water to the air and also because there is less accumulated litter and hence less heterotrophic productivity within the water body lowering oxygen levels. Thus it may be that *Teinobasis* species that live in poorly oxygenated swampy or slow-flowing waters already have broad caudal lamellae (as in the phytotelm-dwelling *T. cf. nigrolutea*) and are to a large extent pre-adapted to life in phytotelmata with higher oxygen concentrations.

Breeding in phytotelmata is uncommon in dragonflies and damselflies (Table 2). Those species exhibiting this trait are not evenly distributed among families and currently only four of the 38 families include phytotelm-breeders. In three of these, Argiolestidae (one of the 20 genera), Aeshnidae (three of the 51 genera) and Libellulidae (eight of the 142 genera), the percentage of genera with phytotelm-breeders is very low. In addition none of the genera included in these three families, with the exception of *Podopteryx*, is completely restricted to phytotelmata. Eighteen of the 31 genera including phytotelmata breeders belong to one of the 144 genera of Coenagrionidae. Fifteen of these are completely confined to phytotelmata. Interestingly all coenagrionid genera with phytotelmata breeders among them are restricted to the 57 genera of the so called “ridge-faced coenagrionids”. However the phytotelm-breeding genera do not form a monophyletic clade within the “ridge-faced coenagrionids” (Figure 6), hence the lifestyle has evidently evolved several times within the family (Ingley, Bybee, Tennessen, Whiting, & Branham, 2012). Independent colonisation of phytotelmata has also been suggested for the libellulid genus *Erythrodiplax* where *E. laselva* and *E. bromeliicola* both have a phytotelm-breeding life style but are more closely related to species breeding in regular aquatic habitats than to each other (Haber, Wagner, & de la Rosa, 2015).

The genus *Papuagrion* is derived from *Teinobasis*, whose species, with the possible exception of one species from the island Pohnpei (Micronesia), are currently all believed to breed in conventional aquatic habitats. In the case of *Papuagrion* we may hypothesise that an ancestral adoption of the phytotelm-breeding lifestyle may have amplified speciation because of increased isolation of populations associated with the discrete nature of the habitat. It has been shown in the Neotropical damselfly *Megaloprepus caerulatus* (Drury, 1782), that a phytotelm-breeding habit combined with low dispersal can lead to strong genetic diversification over relatively short distances, although in this case this only led to poorly defined and non-overlapping taxa when assessed from a morphological point of view (Feindt, Fincke, & Hadrys, 2014). A similar phenomenon may explain the observed high level of speciation in *Papuagrion* where we have currently 26 described species, all apparently closely related. They make up about 25% of the coenagrionid species currently known from New Guinea.

It is interesting to speculate why some families and genera have established themselves in phytotelmata while others failed to do so. It makes sense that families and genera adapted to running water failed (with the notable exception of *Podopteryx*) but it is less clear why no species of Lestidae, a globally occurring family largely restricted to standing water, nor any genus of the “core coenagrionids”, has ever been found in phytotelmata. The majority of lestids and

Table 2. Overview of genera breeding in phytotelmata. Information is based on Corbet (1999), Dow (2014), Fincke (2006), Garrison, von Ellenrieder, and Louton (2006, 2010), Haber et al. (2015), Ingle et al. (2012), Kalkman and Theischinger (2013), Machado (2009), Orr (1994), Orr and Hämäläinen (2013), Paulson and Buden (2003) and Villanueva (2012).

Family	Genus	Range of the species found in phytotelmata	Species in genus	All species (probably) restricted to phytotelmata
Argiolestidae Coenagrionidae	Podopteryx	Australasian	3	Yes
	Anomisma	Neotropical	1	Yes
	Bromeliagrion	Neotropical	3	Yes
	Coryphagrion	Afrotropical	1	Yes
	Diceratobasis	Neotropical	2	Yes
	Leptagrion	Neotropical	17	Yes
	Luzonobasis	Oriental	1	Yes
	Mecistogaster	Neotropical	11	Yes
	Megalagrion	Neotropical	26	No
	Megaloprepus	Neotropical	1	Yes
	Microstigma	Neotropical	3	Yes
	Oreiallagma	Neotropical	5	Yes
	Pandanobasis	Oriental	4	Yes
	Papuagrion	Australasian	26	Yes
	Pericnemis	Oriental	9	No
	Pseudostigma	Neotropical	2	Yes
	Roppaneura	Neotropical	1	Yes
	Sangabasis	Oriental	10	No
	Teinobasis	Australasian	75	No (1 species)
Libellulidae	Camacinia	Oriental	3	No
	Cratilla	Oriental	2	No
	Erythrodiplax	Neotropical	59	No
	Hadrothemis	Afrotropical	8	No
	Libellula	Neotropical	27	No
	Lyriothemis	Oriental	15	No
	Macrothemis	Neotropical	43	No
Aeshnidae	Rhodopygia	Neotropical	5	No
	Gynacantha	Neotropical	88	No
	Indaeschna	Oriental	2	No
	Triacanthagyna	Neotropical	9	No

“core coenagrionids” tend to be found in more open habitats and their larvae tend to have slender lanceolate caudal lamellae, so perhaps they do not possess the appropriate preadaptations needed to colonise phytotelmata. Also surprising is the lack of records of Platycnemididae, which often breed in leafy seepages or marshes in forests and often possess moderately expanded heavily pigmented petiolate gills (Ishida, 1996; Orr & Dow, 2015b, 2016). Again, physiological or behavioural reasons may limit their ability to adapt to phytotelmata but these are not immediately apparent. The predominance of Neotropical and Oriental region genera among the phytotelmata breeders is not surprising as these regions harbour the most extensive forest areas with regular high rainfall.

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